

The genus *Carolia* (Bivalvia: Anomiidae) in the Egyptian Eocene

Amin STROUGO

Faculty of Science, Department of Geology
Ain Shams University, Cairo, Egypt

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SUMMARY — The earliest known occurrence of the genus *Carolia* is in the Lower Eocene, when it appeared simultaneously in Senegal, Egypt and Pakistan. After a period of rapid expansion during the Middle Eocene, it declined in the Upper Eocene and became extinct by the end of that time. In Egypt, where its record is most complete, *Carolia* is represented by five species and one subspecies distributed into six successive stratigraphic levels. From a common parent stock — *Carolia blanfordiana* — two lineages emerged. The first, the *Wakullina* (*Huyella*) *lefevrei* lineage, is characterized by progressive suppression of byssal attachment and development of a secondary hinge line; the second, the *Carolia placunoides* lineage, more conservative, retained the byssus for longer time. The *Pododesmus*-like *Carolia libyca* represents a side-branch of the main stock. A small anomiid — *Tarturia quaasi* n. gen., n. sp. — from the Maastrichtian of Egypt may have given rise to *Carolia* in the Eocene.

RIASSUNTO — [Il genere *Carolia* (Bivalvia: Anomiidae) nell'Eocene egiziano] — La prima comparsa nota del genere *Carolia* avviene nell'Eocene inferiore e si riscontra simultaneamente nel Senegal, in Egitto e nel Pakistan. Dopo un periodo di rapida espansione durante l'Eocene medio, il genere declinò nell'Eocene superiore e si estinse alla fine di quest'epoca. In Egitto, paese nel quale la documentazione è la più completa, *Carolia* è rappresentata da cinque specie ed una sottospecie, distribuite in sei successivi livelli stratigrafici. Da un ceppo originario — *Carolia blanfordiana* — emersero due linee filogenetiche. La prima, ossia la linea di *Wakullina* (*Huyella*) *lefevrei*, è caratterizzata dalla graduale soppressione dell'attacco bissale e dallo sviluppo di una linea umbonale secondaria; la seconda, cioè la linea di *Carolia placunoides*, più conservativa, ha conservato il bisso per un tempo maggiore. *Carolia libyca*, simile a *Pododesmus*, rappresenta un ramo laterale del ceppo principale. Può avere dato origine a *Carolia* nell'Eocene un piccolo anomiide del Maastrichtiano d'Egitto, *Tarturia quaasi* n. gen., n. sp.

INTRODUCTION

Despite the large body of stratigraphical and paleontological information about the Egyptian Eocene which has accumulated since Zittel's 1883 monumental work, the succession of species of the genus *Carolia* Cantraine, 1838 in these rocks has not been recognized by authors. This is because they mostly failed to discern the morphological differences between successive species and lumped them all under one designation, that of *Carolia placunoides* Cantraine, 1838. Even « *Carolia* » *lefevrei* Fischer, 1880, although originally described from the Eocene of our regions, was destined to be forgotten until Desio (1934) rediscovered it in Libya and myself in Egypt (Strougo, 1976, 1977). In the last mentioned work I had also proposed the new subspecies *C. placunoides foraminifera* from the terminal Eocene of the Fayum.

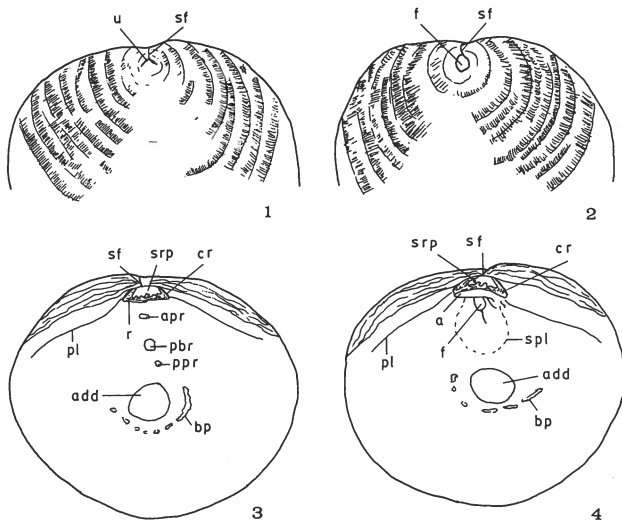
In the course of the past few years, extensive work on the Eocene exposures across the country led to the discovery of several other species of *Carolia*.

Thus *C. blanfordiana* (Cox, 1938) was lately reported from the Lower Eocene succession at Luxor by Strougo & Hassaan (in press) and the present investigation adds two more species to the record, one of which is new and the other previously only found in Libya. Because of the narrow range in time of most of the species treated, it now appears that *Carolia* is one of the most reliable groups for working out our Eocene succession.

With a nearly uninterrupted record from the earliest to the latest occurrence of the genus, unequalled in the world, Egypt seems to be the favorite place for the study of the evolution of this group during the Eocene Epoch. As we shall see, it is even likely that the ancestral stock of *Carolia* may have frequented our Maastrichtian coastal waters.

MORPHOLOGY OF THE CAROLIA SHELL (Text-fig. 1)

The shell of *Carolia* is roughly circular in outline, with a plane or undulate margin, a slightly concave



Text-fig. 1 - Morphology of the *Carolia* shell. 1, 3, exterior and interior of left valve; 2, 4, exterior and interior of right valve. a, apophysis; add, adductor muscle scar; apr, anterior pedal retractor; bp, branchiopallial muscles; cr, 'crural' ridges; f, foramen; pbr, posterior byssal retractor; pl, pallial line; ppr, posterior pedal retractor; r, resilifer; sf, supra-dorsal fissure; spl, line of secondary pallial attachment; srp, supraresilifer plate; u, umbo.

right (lower) valve, and a slightly convex left (upper) valve, the latter somewhat overlapping the dorsal edge of the under valve. The umbo of the left valve is distinctly removed backward from the margin but joined to it by supradorsal fissure. A similar fissure occurs in the right valve but here the umbo is obliterated. The sculpture is made of fine, discontinuous, vermicular radial threads.

Seen from the interior, the shell has a large, circular, nearly central adductor scar rimmed on three sides by a host of very small impressions. These are much like the branchiopallial insertions described in *Placuna placenta* (Linné) by Woodward (1855). The pallial line, though probably continuous, is only discernible in the dorsal side of the valves. A line of secondary pallial attachment, present only in the right valve, probably circumscribed the area occupied by the visceropedal mass. Together with the branchiopallial muscles it would indicate the extent to which the mantle lobes could be withdrawn (Yonge, 1977).

The left valve bears three more muscle attachments commonly arranged in a linear pattern between the adductor scar and the resilifer. These are the small anterior and posterior pedal retractors, separated by the larger scar of the posterior byssal retractor. The byssus is a markedly large calcified plug passing through a wide foramen (sometimes an embayment) in the under valve. Eventually the byssal muscles may atrophy and the foramen sealed off its former presence being indicated by a linear or sinuous suture internally and a plugged orifice externally. The ligament of the right valve is seated upon a massive, stalked apophysis while in the left valve it is received in a deep triangular groove (resilifer). The edges of the ligamental area are raised into thin, lamellar, obtuse ridges recalling the crural ridges of *Placuna* Solander. As with the umbo, these are displaced from a marginal position by supradorsal shell secretion. From the roof of both crurum and resilifer, a shelf-like plate (whose function is not clear) is developed carrying coarse irregular nodosities near their distal ends. To this structure Abbass (1961 (1965)) gave the name of supraresilifer plate. During adduction of the valves these plates meet by their distal ends at various angles, most frequently at right angle.

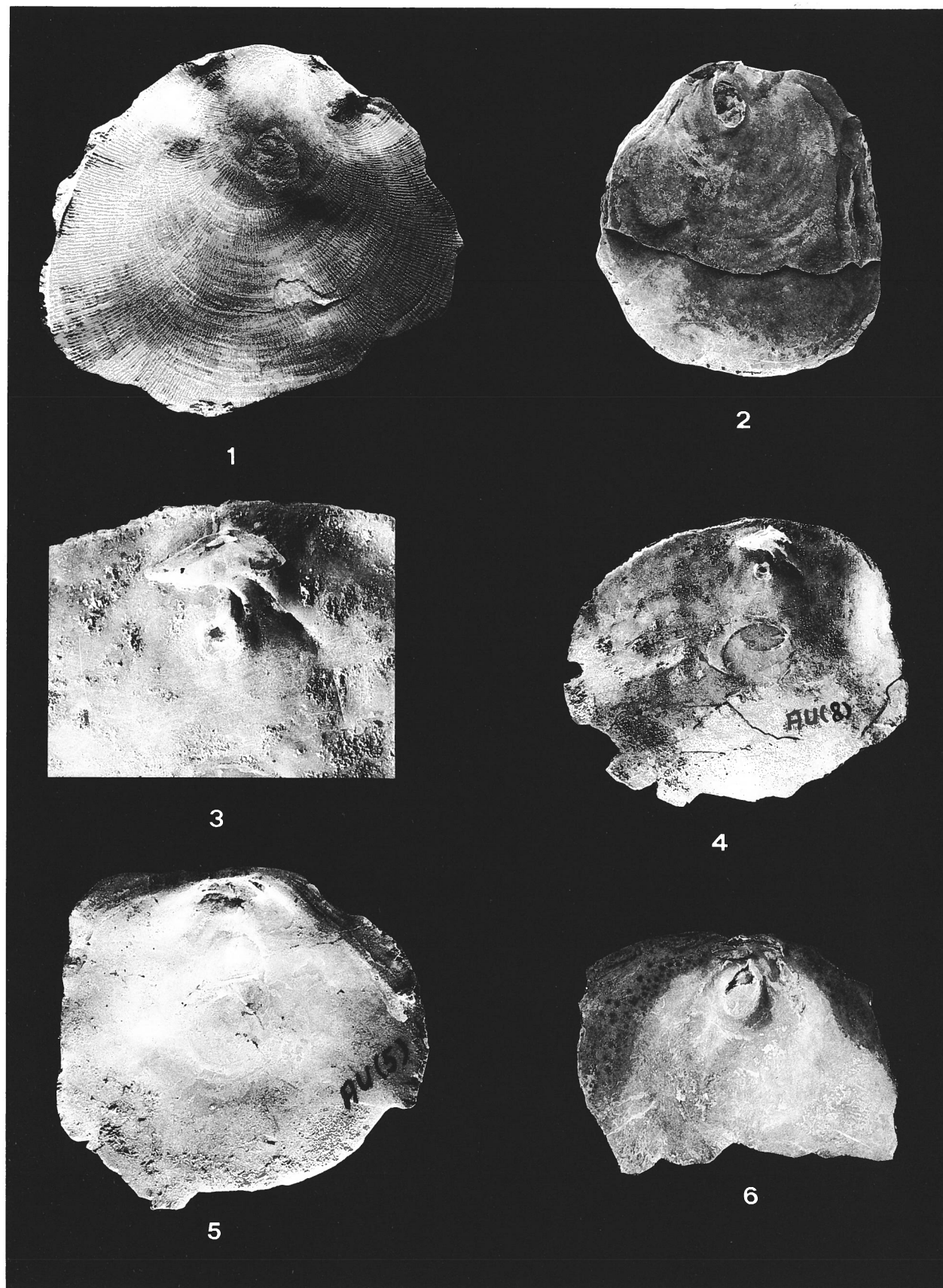
ORIGIN OF CAROLIA

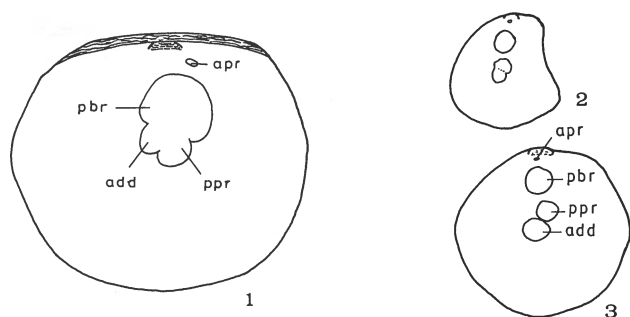
In 1902, two specimens of a very small bivalve obtained from the Maastrichtian 'Overwegischichten' in the Western Desert of Egypt were considered by Quaas to belong to the genus *Carolia*. The specimens exhibited the typical surface sculpture of the genus but had mostly unrecognizable internal characters. Quaas has therefore satisfied himself by designating them *Carolia* sp.. This fossil was never subsequently reported either inside or, as far as I am aware, outside Egypt and simply sank into oblivion. *Carolia* being reputed to be a strictly Eocene genus, the importance of restudying this Cretaceous anomid is obvious. It would confirm or correct the traditional stratigraphic range of *Carolia* and hence would permit to define more accurately the relationship between this genus and the 'Overwegischichten' fossil.

During the past few years I have collected several examples of that very rare fossil from Maastrichtian

EXPLANATION OF PLATE 1

- Figs. 1-2 - *Carolia blanfordiana* (Cox, 1838). Outer views of left and right valve, Gebel Gurnah, Lower Eocene, x 2.
 Figs. 3-4-5-6 - *Carolia fischeri* n. sp.. 4) right valve, inner view, holotype, Gebel El Têr, north of Minia, lower Middle Eocene, x 0.5; 3) the same showing details of byssal foramen and apophysis, x 1.5; 5) left valve, inner view, Gebel El Têr, north of Minia, lower Middle Eocene, x 1; 6) right valve, inner view of hinge area, Gebel Abu Genah, north of Beni Hasan, lower Middle Eocene, x 1.





Text-fig. 2 - Patterns of musculature in (1) *Tarturia quaasi*, and (2, 3) immature shells of *C. placunoides placunoides*. For key to lettering, see text-fig. 1.

strata cropping out in Quseir and in the Kharga-Dakhla divide. The characters of its shell, though precluding its identification with *Carolia*, suggest a close relationship between the two forms whereby '*Carolia*' sp. would have given rise to the true *carolias* in the Eocene. Unfortunately the immediate ancestor of *Carolia blanfordiana* — the earliest definite representative of the genus to date — is probably still buried in Paleocene and basal Eocene rocks. Until this ancestor has been dug out and studied, the phylogenetic relationships suggested further must be considered as speculative. But first, it is worth starting with a brief description of the shell of '*Carolia*' sp. as it turned out to represent a new genus and which I here name *Tarturia quaasi* n. gen., n. sp.. The generic name is from the plateau of Abu Tartur, to the northwest of the Kharga oasis, and the specific name is in honor of A. Quaas who gave the first description of this species.

T. quaasi exhibits most of the gross morphological features of a primitive *Carolia*, even though it attains the unimpressive size of 15 mm (Pl. 2, figs. 6, 7 and text-fig. 2-1): shell compressed; outline regular; dorsal margin nearly straight; commissure of the valves in a plane; exterior foliaceous, with fine irregular radial threads; large, permanent byssal opening; ligament carried by a prominent apophysis in the right valve, set in a triangular resilifer in the left; thin, projecting « crural » ridges; three retractor scars.

The most distinctive feature of *T. quaasi* lies in the arrangement of the retractor scars in the shell

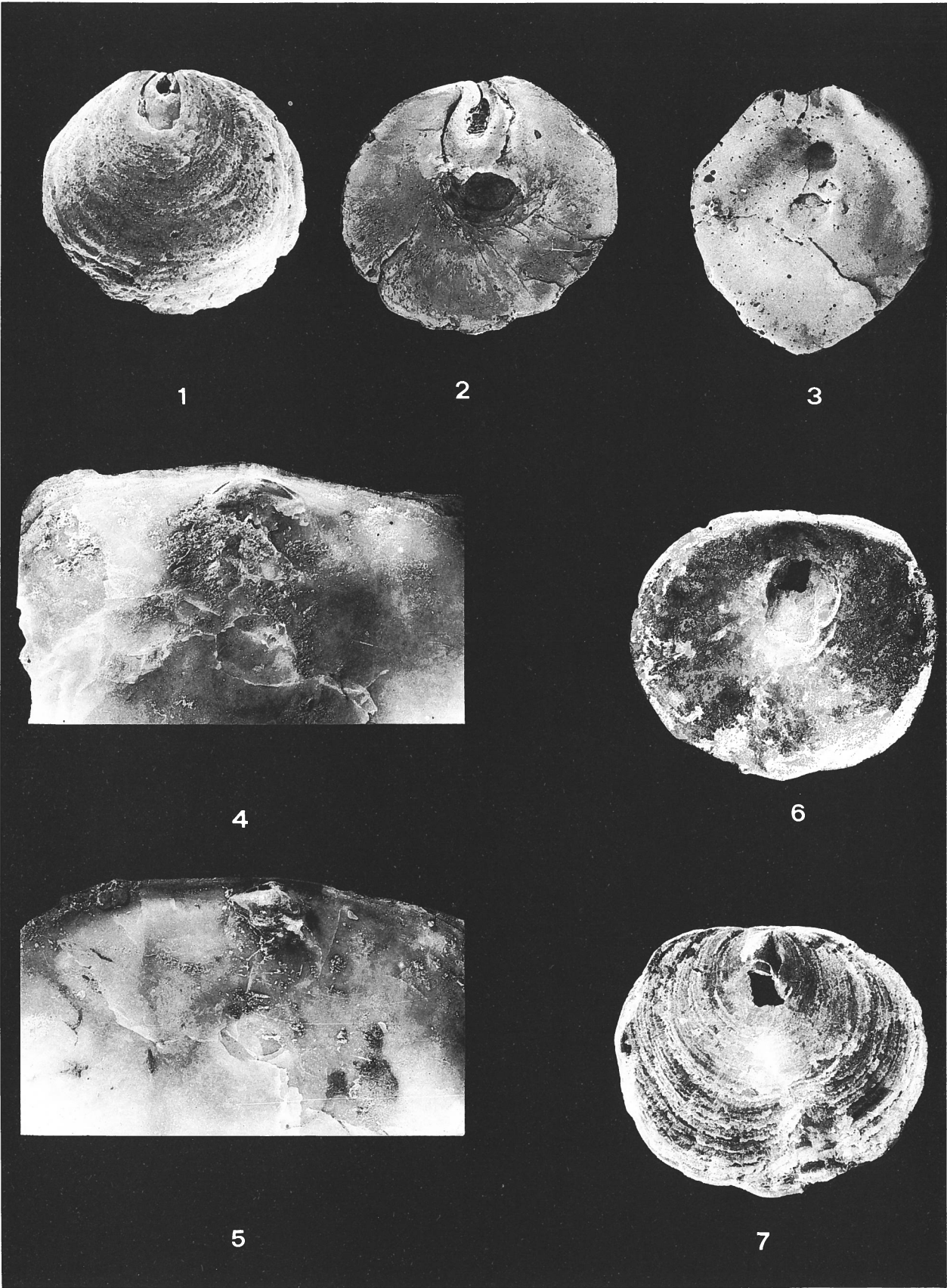
interior. While in *Carolia* these are well individualized and separate, in *T. quaasi* the two posterior retractors immediately adjoin the adductor so that the three form one large continuous muscular impression. This impression, however, shows three strong constrictions at the margin which, we can presume, indicate the boundaries between the three contiguous scars. It thus appears that the adductor and the posterior pedal retractor scars are subequal in size whereas the byssal scar is conspicuously larger. The anterior retractor scar, on the other hand stands by its own below the anterior end of the resilifer.

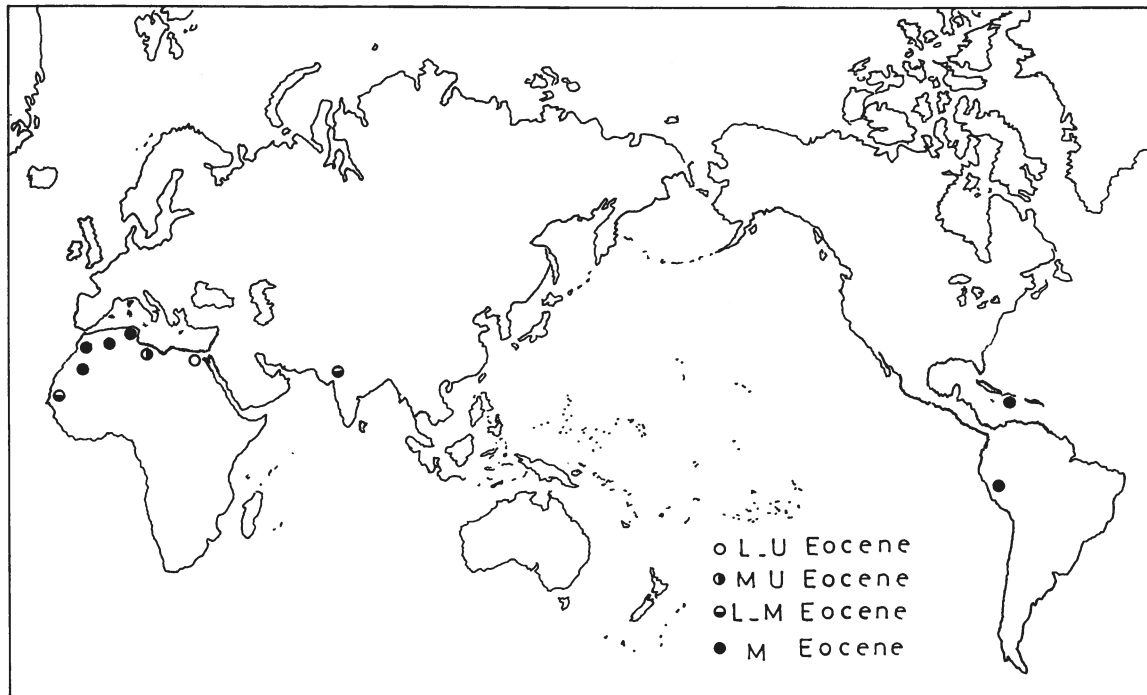
In *Carolia* the retractor scars, including the byssal retractor, are smaller than the adductor; in the adult shell they are sometimes even obsolete. This character alone sets *T. quaasi* apart from *Carolia*. Nevertheless the true affinities between the two forms are revealed when we compare *T. quaasi* with the immature shells of *C. placunoides placunoides*. The smallest specimen of that fossil examined is about 25 mm in diameter (text-fig. 2-2). It shows a small posterior retractor lying with diffuse contact above an equal-sized adductor; the byssal retractor, much larger, is slightly separated from the two while the small anterior retractor lies below the resilifer. In the right valve the byssal opening has the form of a wide, circular embayment. In another specimen, 40 mm in diameter, the posterior retractor and the adductor still lie side by side (text-fig. 2-3) but exhibit distinct outlines; the byssal impression is still the largest. The right valve has not been observed. Above 50-60 mm, the byssal retractor ceases to grow or even begins to atrophy and is supplanted by the growing adductor. In the right valve a varying foramen lies directly below the apophysis.

Considerable departures from what has just been described can be observed in other individuals of *C. placunoides placunoides* as there is no rigorous correlation between shell size and degree of development of the byssal opening, the latter being in turn governed by the size of the byssal retractor (Strougo, 1971, 1977). Therefore the above figures are intended only to show the type of modifications brought about in the shell of this fossil in the course of its ontogenetic development, and it is clear from these figures that in the immature shell of *C. placunoides placunoides* the musculature, though very close to that of

EXPLANATION OF PLATE 2

- Figs. 1-2-3 - *Carolia libyca* Cox. 1962. 1-2) right valve, outer and inner views, Gebel Homret Shaiboun, uppermost Middle Eocene, x 1.5; 3) left valve, inner view, Gebel Qattamia, uppermost Middle Eocene, x 1.5.
Figs. 4-5 - *Wakullina (Huyella) lefevrei* (Fischer, 1880). Left and right valves showing hinge line and ligamental area, Gebel Qarara, upper Middle Eocene, x 1.
Figs. 6-7 - *Tarturia quaasi* n. gen., n. sp. Left valve, inner and outer views, holotype, Abu Tartur Plateau, Maastrichtian, x 4.



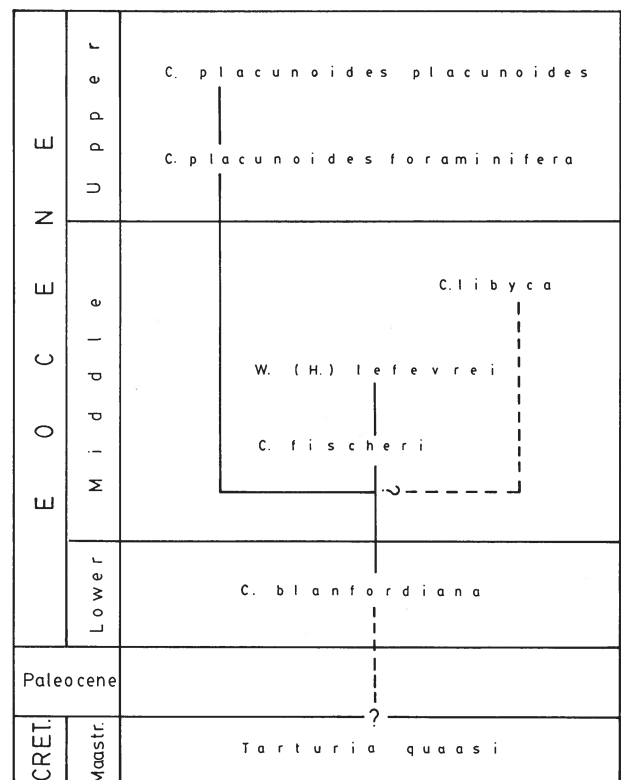
Text-fig. 3 - Geographical and stratigraphical distribution of *Carolia*.

T. quaasi, is identical to that of *Anomia*, as anciently assumed by Fischer (1880). But *Carolia* differs from *Anomia* in several other respects.

T. quaasi would have certainly been referred to *Anomia* had it not the regular outline and the sculpture of *Carolia*, and a musculature that is more compact than in *Anomia*. The three genera, doubtless, are very close and *T. quaasi* which presumably has just begun to diverge from *Anomia* and to be shaped like a small *Carolia* could represent the link between the two genera, the « *Anomia*-like stage », the existence of which was predicted over a century ago by Fischer (1880).

EVOLUTIONARY HISTORY OF *CAROLIA* IN EGYPT

As we can now discard the Maastrichtian '*Carolia*' sp. from our discussion, the earliest known occurrence of *Carolia* is in the Lower Eocene when it seems to have appeared without recognizable immediate ancestor simultaneously in Senegal, Egypt, and Pakistan. During the Middle Eocene the group undergoes rapid expansion extending its range to many new places as Libya, Tunisia, Algeria, Morocco, Mauritania, Jamaica, and may be even Peru (text-fig. 3). Judging by the present literature, no significant « bursts » of speciation appear to have taken place during the geographic expansion of the group. Apparently this expansion has also been of short duration because in the

Text-fig. 4 - Inferred phylogeny of the *Carolia* stock in the Egyptian Eocene.

Upper Eocene *Carolia* suffered severe reduction retreating back into what could have been its headquarters, northeast Africa, where the latest representatives of the genus occur.

As said in the introduction, we can grasp quite a bit of the evolutionary history of *Carolia* by studying the Egyptian Eocene where representatives of the genus are numerous, short-ranged and succeed each other virtually without interruption. *Carolia* is represented in our regions by five species and one subspecies distributed into six successive stratigraphic levels (text-fig. 4). Their evolution is characterized by two trends in the stabilization of the shell onto the substrate. The first trend manifests itself in what we can call the *Wakullina* (*Huyella*) *lefevrei* lineage, and the second in the *Carolia placunoides* lineage. A third possible trend, poorly documented at present, is represented by the *Pododesmus*-like *Carolia libyca*. The following remarks on phylogeny are inferred from morphological affinities and, sometimes, gradational changes among species. They are however tentative and generalized as some of the Egyptian species did not evolve *in situ* but were introduced into the area by migration and therefore the early part of their history remains unknown.

The earliest occurrence of the genus *Carolia* in Egypt is in the upper beds of the Thebes Formation of Lower Eocene age, at Gebel Gurnah opposite Luxor. The species, previously unrecorded from Egypt, was lately discovered by Strougo & Hassaan (in press) and identified with the Upper Laki (Lower Eocene) and Lower Khirthar (Middle Eocene) *Parinomya blanfordiana* Cox, 1938 which should now be regarded as a true *Carolia* as suggested by Strougo (1977).

Carolia blanfordiana, with its small size (maximum diameter, 55 mm), poorly defined marginal undulations, large and permanent byssal foramen and juxtaposed supradorsal ends (See pl. 1, figs. 1, 2), exhibits all the primitive attributes of the genus and is considered to represent the main parent stock from which later species were descended.

The Wakullina (*Huyella*) *lefevrei* lineage - Two successively derived species constitute the *Wakullina* (*Huyella*) *lefevrei* lineage. These are, in ascending order, *Carolia fischeri* n. sp. (1) and *W. (H.) lefevrei* Fischer, 1880. Evolving from *C. blanfordiana* in the Middle Eocene, this dynamic group undergoes outstanding evolutionary change so that its later member came to differ in the most striking way from the parental stock. More moderate changes, however, are noticed in *C. fischeri* from the Samalut For-

mation of early Middle Eocene age. In this species the shell has increased to 90 mm in diameter, slight to moderate undulations appear near the margin, and the foramen is of varying size, usually closed proximally in fullgrown specimens (Pl. 1, figs. 3, 4, 5, 6). In the later derived *W. (H.) lefevrei*, these characters were further accentuated: conspicuous curvature of the valve margin, precocious suppression of the byssal apparatus and closure of the foramen. Additionally, a secondary hinge line is created, and the beak moved to a marginal position while the maximum shell size has jumped to 130 mm (Pl. 2, figs. 4, 5). In brief, *W. (H.) lefevrei* constitutes a remarkable case of convergence with the Recent *Placuna sella* Gmelin which lives unattached (except for a brief post-larval period) on the surface of mud flats in the Indian Ocean (Yonge, 1977). *W. (H.) lefevrei* may have had a similar mode of life. The rare presence of a suture line below the apophysis ending distally with a very small plugged orifice and the eventual occurrence of three small retractor scars between the adductor and the resilifer show that in some individuals of *W. (H.) lefevrei* the byssus was retained for a longer period and show that this species is closely related to and undoubtedly descended from *C. fischeri*. That nevertheless it should not be included in the genus *Carolia* is supported by the development of a hinge line, to mention but this very character. The importance of the hinge line in the Anomiacea has been emphasized by Yonge (1977) who used it as a major asset for the erection of the new family Placunidae.

Another possible descendant of *C. fischeri* is a short-lived species, *C. libyca* Cox, 1962, originally described from Libya and here reported for the first time from Egypt where it seems to replace *W. (H.) lefevrei* in the uppermost beds of the Middle Eocene although it was supplanted - at the beginning if the Upper Eocene - by the *C. placunoides* lineage. In *C. libyca*, modification of the shell takes place along a different line from the one just described. Here we notice a fuller exploitation of the ventral shift of the byssal opening begun in *C. fischeri*, leading to a more intimate attachment of the shell to the substrate. The foramen, now strongly submerged in the shell, is more or less widely open to the interior but « closed or reduced to a very small orifice externally » (Cox, 1962). *C. libyca* thus combines with the three retractor scars (not mentioned in the original description but observed in my specimens) of *Carolia* a foramen that appears to be more like that of *Pododesmus* (Pl. 2, figs. 1, 2, 3). In effect, the virtual loss of contact with the exterior suggests that the calcified byssus must have fused with the walls of the foramen so

(1) In honor of P. Fischer who wrote the first comprehensive account on *Carolia*.

that the under valve was directly cemented to the substrate as it is the case in *Pododesmus* and *Placunanomia*. Unfortunately the available material does not permit to evaluate properly this assumption. But it would seem that Dall's 1898 statement « From *Carolia* to *Pododesmus* is a short step » is not as illusory as Douville's 1921 evolutionary scheme of the Anomiacea would let us suppose.

The *Carolia placunoides* lineage - While *W. (H.) lefevrei* and *C. libyca* appear as an 'atypical' progeniture of the *Carolia* stock, a more conservative line manifests itself in the Upper Eocene with two successively derived subspecies, *C. placunoides foraminifera* Strougo, 1977 followed by *C. placunoides placunoides* Cantraine, 1838. These most closely resemble *C. blanfordiana* from which they differ only by their much larger sizes (up to 180 mm in typical *placunoides*) and gentle marginal undulations. *C. placunoides placunoides*, moreover is characterized by overlapping supradorsal ends and a more or less impermanent byssal foramen. The latter, when it begins to close, remains confined under the apophysis, i.e., closure proceeds gradually dorsalward. Clearly, none of the Middle Eocene species described so far could have produced this lineage. It was probably derived from *C. blanfordiana* (or a closely related species) which, maybe in Algeria (the *C. placunoides* (jeune) of Flandrin (1938) could be a *blanfordiana*), but at all events in Pakistan, persisted into the Middle Eocene (Cox, 1938; Eames, 1951). Therefore *C. placunoides* s.l. is not an endemic species but it was introduced into the area by migration.

C. placunoides foraminifera, with its permanent byssal foramen and juxtaposed supradorsal ends appears less evolved than *C. placunoides placunoides* and is probably the direct descendant of *C. blanfordiana* later giving rise to *C. placunoides placunoides*. Paradoxically, in Egypt the stratigraphic ranges of the two subspecies would indicate just the opposite relationship. In the absence of a critical study of the carolias elsewhere, this conflicting evidence cannot be resolved. Bearing in mind that *C. placunoides* s.l. is an immigrant species I would assume that it had appeared somewhere in the Tethys since the late Middle Eocene (several Middle Eocene occurrences of this species are reported in the literature) but could not compete with the species then established in Egypt (*W. (H.) lefevrei*). The disappearance of that species toward the end of the Middle Eocene and its replacement by the very rare *C. libyca* gave the opportuni-

ty to *C. placunoides placunoides* succeeded by *C. placunoides foraminifera* to invade the area. The radical paleogeographical changes which affected Egypt at the end of the Upper Eocene brought the history of *Carolia* to an end.

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